ACTIVITY PATTERNS OF FEMALE RUFFED GROUSE DURING THE BREEDING SEASON

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Ruffed Grouse (*Bonasa umbellus*) are difficult to observe for extended periods in the wild. Consequently, despite the considerable research attention this bird has received (e.g. Bump et al. 1947, Gullion and Marshall 1968, and others), few precise data are available concerning its activity patterns. Recent radiotelemetry studies in Minnesota (Archibald 1973 and several studies cited therein) have increased our knowledge of this aspect of the Ruffed Grouse's behavior but activity patterns of female Ruffed Grouse during the breeding season remain poorly documented. This paper reports a radiotelemetry study of female Ruffed Grouse activity patterns from pre-incubation through post-incubation periods at the University of Minnesota's Cedar Creek Natural History Area located about 45 km north of Minneapolis, Minnesota.

METHODS

Field observations were made from 1 April–30 June 1971 and 1 April–7 July 1972. The Ruffed Grouse population was at a peak level during this investigation. Spring counts of drumming males totaled 30 and 28 on the square mile study area in 1971 and 1972 respectively.

Female Ruffed Grouse were captured by baited lily-pad traps (Gullion 1965), nest traps (Weller 1957), dip-netting on the nest (Robel et al. 1970), and by nightlighting (Huempfner et al. 1975). Hens captured on their nests were handled in the field to minimize the time they were kept off the eggs. All others were placed in burlap bags and transported to the Cedar Creek laboratory where they were weighed, sexed, aged, leg-banded, and equipped with a 24–26 g transmitter similar in harness design to one described by Brander (1968). Expected transmitter life ranged from 50–75 days but usually birds were recaptured and fitted with new transmitters before this time. All birds were released at the point of capture.

Radio-marked grouse were monitored with an automatic radio-tracking system (Cochran et al. 1965). Two towers 0.8 km apart support directional receiving antennas continually rotating at 1⅓ rpm. During each antenna revolution, radio signals emanating from the transmitter equipped grouse were received by the antennas. Signals were relayed to a centrally located laboratory and, after amplification and modification, were recorded on 16 mm film as degree bearings for each tower. These bearings were used to determine the location of the bird by triangulation. With the use of a microfilm reader, an activity designation (active, inactive, or unknown) was determined at 15 min intervals for each bird. Marshall and Kupa (1963) determined that the pitch of the radio signal changed as a grouse moved about. This change in signal pitch associated with activity is reflected as irregularities in signal peaks on the film record (Sargeant et al. 1965). During each 15 min period (except during incubation) a grouse was considered active if 4 or more signals exhibited these irregularities, or if a change in bearing of 1 or more degrees

TABLE 1

PERCENTAGE OF TIME FEMALE GROUSE WERE ACTIVE

		Pre-incubation		Incubation		Post-incubation			
						With Brood		Without Brood	
Bird No.	Age	No. Days	% Time Active	No. Days	% Time Active	No. Days	% Time Active	No. Days	% Time Active
1657	J	28	44.5	27	4.5	20	52.7	—	—
1690	J	36	51.2	25	4.8	—	—	—	—
1691	A	35	47.3	26	3.5	26	51.5	—	—
1695	J	36	48.7	25	3.9	9	58.4	—	—
1698	J	—	—	—	—	—	—	29	67.5
1699	J	—	—	—	—	8	56.9	—	—
2200	A	—	—	—	—	30	58.5	—	—
2201	J	—	—	—	—	—	—	29	60.5
2202	—	—	—	—	—	—	—	18	51.0
2210	J	45	47.9	10	4.9	—	—	—	—
2219	J	—	—	21	4.1	—	—	—	—
2235	A	—	—	25	3.1	—	—	—	—
2238	J	46	37.3	26	4.4	—	—	—	—
2239	J	43	55.6	26	5.8	30	54.4	—	—
2241	J	37	41.7	17	4.1	—	—	43	59.0
2246	A	36	48.4	26	3.4	18	47.1	—	—
2248	J	—	—	25	4.7	—	—	—	—
Mean		38	46.9	23	4.3	20	54.2	30	59.5

occurred for either tower. During the incubation period activity changes were determined to the nearest minute.

Data for each bird were divided into pre-incubation, incubation, and post-incubation periods and were analyzed in 2 ways using the University of Minnesota's Control Data 6600 computer system. First, the sampled activity for each day was plotted giving every 15 min interval an activity symbol (active, inactive, or unknown). This illustrated day-to-day periods of activity. Second, the percentage of time a bird was active during each 15 min interval over a given time period (pre-incubation, incubation, or post-incubation) was plotted, giving a composite 24-h day comprised of data for all days during a time period. This illustrated activity trends throughout the specified period.

All times given are C.S.T.

RESULTS

Activity data were obtained from 17 female Ruffed Grouse during the study. Table 1 summarizes the percentage of time the birds were determined to be active during the pre-incubation, incubation, and post-incubation periods. Percent activity tended to be greater during the post-incubation period than the pre-incubation period, perhaps due to increased daylength. Hens with

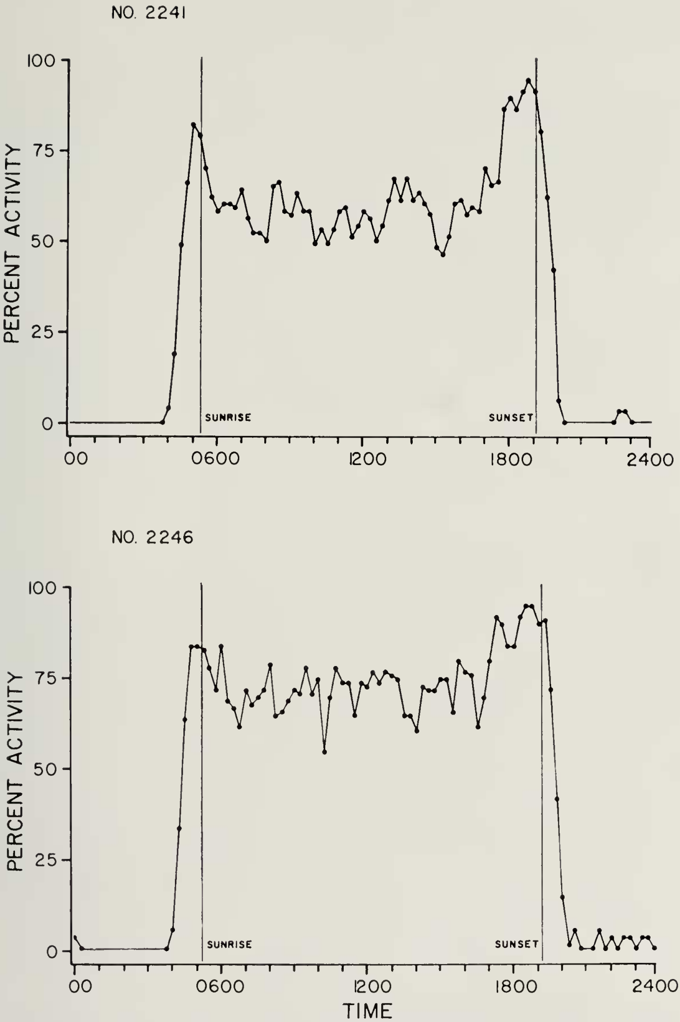

FIG. 1. Temporal distribution of percentage of 15-min intervals active during the pre-incubation period for Hens 2241 and 2246.

broods tended to have a lower percent activity than those without broods. During incubation, activity was greatly reduced and limited to a few short feeding periods each day.

No relationship between age (juvenile 10–12 months old, adult 22 months or older) and activity levels was evident except during incubation when the 3 adult hens monitored exhibited the 3 lowest activity levels. There was no apparent relationship between color phase of the birds and activity levels.

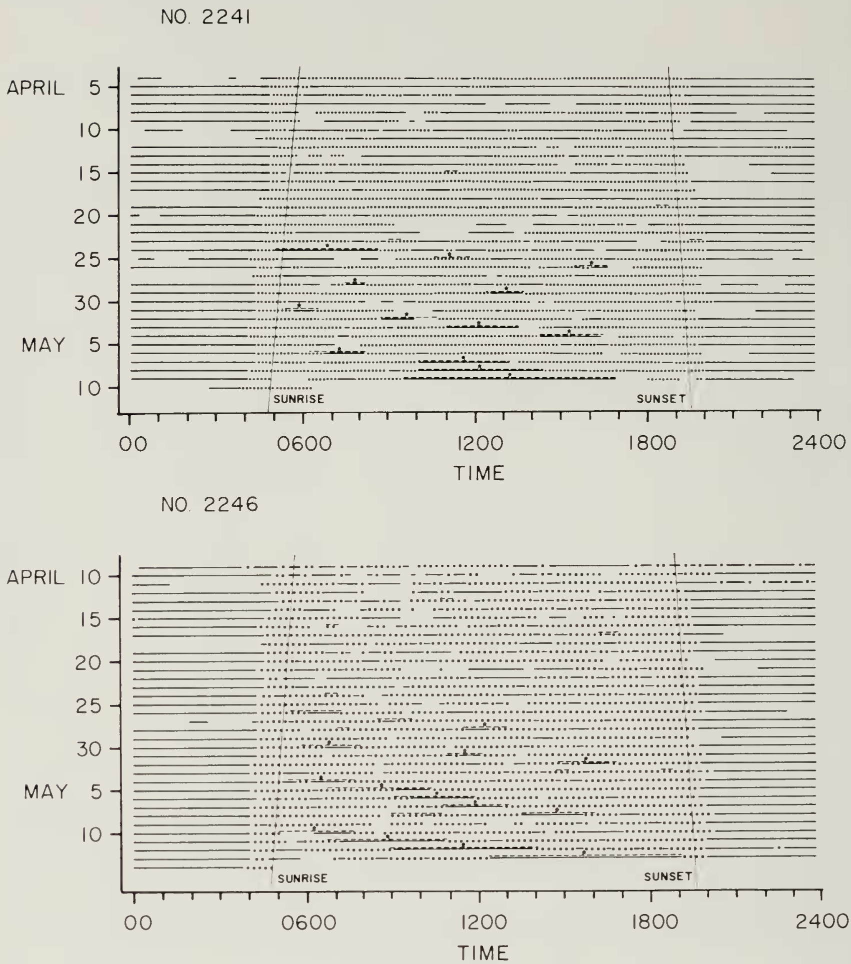

FIG. 2. Daily periods of activity, visits to the nest site, and probable egg laying periods for Hens 2241 and 2246 during the pre-incubation period (—— = inactive, · · · = active, – – – = hen at or near nest site, * = nest visits during which egg laying probably occurred, blank = no data).

Pre-incubation.—The temporal distribution of percentage of 15 min intervals active during the pre-incubation period was determined for 9 hens (Maxson 1974). Fig. 1 gives 2 examples of these data. Activity seldom occurred at night. Peaks of activity were closely associated with sunrise and sunset. The evening peak was greater than the morning peak for all hens.

Activity levels during the day fluctuated and were variable among birds. Daytime activity seldom fell below the 50% level and sometimes exceeded the dawn-dusk peaks for short periods.

Fig. 2 illustrates daily activity for 2 hens. Daytime activity, for all hens combined, began prior to sunrise on 302 of 306 (98.7%) grouse-days and ceased after sunset on 296 of 310 (95.5%) grouse-days. Activity usually began 30–60 min before sunrise and in most cases ceased 15–45 min after sunset. The exact timing of activity onset and cessation varied slightly from day to day and was likely influenced by weather changes.

Egg laying.—By coordinating activity and location data for 8 hens from which nearly continuous telemetry records were obtained, it was possible to determine when they had visited their nest sites prior to the beginning of incubation. I assumed that eggs were laid during some of these visits, although I could not determine exactly when egg laying occurred during a nest visit. Fig. 2 indicates all occasions whan Hens 2241 and 2246 were known to be at or near their nest sites as well as probable egg-laying visits. Both hens had 13-egg clutches.

Visits to the nest followed a definite pattern. Hens seldom visited the nest site prior to the onset of egg laying, suggesting that nest construction was not very time-consuming. Once egg laying began, hens were rarely near the nest site except during presumed laying visits. During laying visits they normally remained inactive on the nest from 1 to several hours. As the clutch approached completion, hens tended to remain on the nest for longer periods. Egg-laying visits occurred 1–5 days in succession at intervals ranging from 25–30 h. Eggs were laid slightly later during each day of a laying sequence. When the next egg of a sequence appeared to be due sometime after the end of evening activity, the egg was not laid until the following morning thus beginning another sequence with the usual 25–30 h interval between eggs. The number of days in a laying sequence varied both among birds and for the same individual as well. As examples, the laying sequences for several hens were the following: Hen 2210, 1-2-2-3-4; Hen 2239, 2-3-3-3; Hen 2241, 3-2-4-4; Hen 2246, 1-3-5-4 (numbers indicate the number of consecutive days during which an egg was laid while hyphens indicate the skipping of a day between eggs). Similar overall patterns of egg laying were observed for all hens monitored.

Since renesting by Ruffed Grouse in the wild has been proven on only 1 occasion (Barrett 1970:79–81), evidence is presented here that Hen 1695, which had only 8 eggs and did not begin incubating until 20 May (several days later than the other hens), successfully renested. Fig. 3 illustrates the activity of this hen during the pre-incubation period. Although some gaps occur in these data, the probable laying times of 7 eggs were determined.

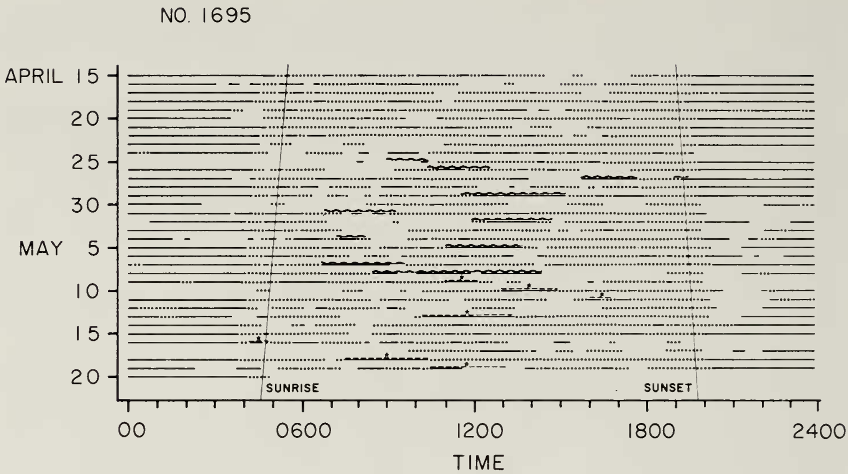

FIG. 3. Daily periods of activity, visits to the nest site, probable egg laying periods, and probable visits to a previous nest site for Hen 1695 during the pre-incubation period (—— = inactive, · · · = active, - - - = hen at or near nest site, * = nest visits during which egg laying probably occurred, ~ = hen at or near probable first nest site, blank = no data).

The remaining egg may have been laid during the data gap on the morning of 17 May. The first egg of the clutch was apparently laid on 9 May. Prior to this date a pattern of activity similar to that occurring during egg laying was evident. Inactive periods possibly associated with egg laying are indicated in the figure. The telemetry record indicates that these were all at a single location approximately 160 m from the nest. This suggests that an earlier nest had been established on 25 April (about the same time other hens were beginning to lay) and that up to 10 eggs had been laid. On 8 May, prior to the onset of incubation, they were likely destroyed by a predator. The second nest was apparently established the following day on 9 May.

Examination of the nest visit pattern suggests that the original clutch size would have been 14 (assuming that the first egg was laid on 25 April and the 14th was laid on 13 May). No nest visits occurred on 14 and 15 May. This was the only hen which skipped more than 1 day between laying sequences. Probably this time lag was required for formation of additional eggs. Remating may have been necessary as well.

Incubation.—Activity patterns during the incubation period were determined for 12 hens. Field observations and the telemetry record indicated that hens normally left the nest only to feed. The number of nest absences per day varied from 1–5 but was most often 2 or 3 (Table 2). While no hen

TABLE 2

NUMBER OF DAYS HENS HAD FROM 1 TO 5 NEST ABSENCES[1]

Bird No.	Total No. Nest Absences Per Day				
	1	2	3	4	5
1657	—	5	11	—	—
1690	—	4	8	7	—
1691	1	6	9	4	—
1695	1	11	5	2	2
2210	—	6	1	—	—
2219	—	1	6	—	—
2235	—	11	2	—	—
2238	—	2	8	2	—
2239	1	11	4	2	—
2241	—	5	7	—	—
2246	—	11	7	—	—
2248	—	—	7	6	2
TOTAL	3	73	75	23	4

[1] Includes only days on which nearly constant telemetry records were obtained.

had the same number of absences per day throughout the incubation period, some (e.g. Hen 2235) were fairly consistent in making 2 feeding trips per day whereas others (e.g. Hen 2238) usually made 3 trips.

The length of 590 nest absences was determined to the nearest minute and the total minutes off the nest per day was calculated for 177 grouse-days. Table 3 summarizes these data and indicates intra- and inter-bird variability. Eight birds had mean absence lengths of 18–24 min. Hen 2239 had 1 unusually long absence of 197 min. This was more than twice the length of the longest absence recorded for any of the other birds. Possibly this hen was disturbed by a predator while feeding and failed to return to the nest in the usual amount of time. Excluding the 197 min absence, Hen 2239 had absences ranging from 14–65 min (mean 37 min). On days hens were absent only twice, the last absence tended to be longer than the first (44 of 73 grouse-days (60%)). In contrast, of 102 days when hens were absent more than twice, the last absence of the day was the longest on only 42 (41%) occasions.

The total number of minutes off the nest varied from day to day for individual hens. Overall, juvenile hens spent more time off the nest than adults (juvenile mean 66 min, adult mean 46 min) suggesting that adults are more efficient incubators. Among birds, there was no consistent relationship between mean absence length and mean total minutes off the nest per day. Also, hens did not consistently increase or decrease nest attentiveness as incubation progressed except during the last day or 2 when eggs were in the process

TABLE 3

SUMMARY OF NEST ABSENCES DURING THE INCUBATION PERIOD

Bird No.	No. of Recorded Absences[1]	Absence Length (min)		Total Time Off Nest Per Day (min)[2]	
		Mean	Range	Mean	Range
1657	49	28	17– 77	70	47– 93
1690	65	19	8– 56	57	40– 77
1691	59	15	7– 32	41	18– 58
1695	64	21	6– 42	58	41– 96
2210	19	34	20– 82	65	46– 81
2219	32	24	11– 37	62	46– 76
2235	38	24	12– 59	46	34– 76
2238	50	22	13– 41	66	45– 93
2239	47	40	14–197	90	28–242
2241	37	23	5– 32	60	43– 81
2246	57	21	8– 37	52	33– 77
2248	73	19	7– 33	70	53–100

[1] Includes only absences where departure and return were determined to the nearest minute.
[2] Includes only those days on which nearly constant telemetry data were obtained.

of hatching. At that time the birds seemed restless and were frequently active at the nest site for short periods.

Daily activity of 3 hens is illustrated in Fig. 4. All hens demonstrated a shift in the temporal distribution of the first activity period of the day as incubation progressed. Activity usually began prior to sunrise during the early stages of incubation but later the start of activity was delayed as much as 4–5 h after sunrise. The beginning of this shift in activity ranged from 20–30 May in 1971 and from 16–25 May in 1972. Synchrony among hens was evident in 1972 when 5 of 7 began this shift during 22–25 May. The shift began during different stages of the incubation period (from the 4th to 19th day) for different hens. No relationship was evident between the onset of the activity shift and any trend in average hourly temperature, wind velocity and direction, or amount and time of occurrence of precipitation.

A possible relationship between plant phenology and the activity shift was noted in 1972 when phenologic events were studied in detail. During the week of 18–25 May the leaves of most trees and shrubs reached full size. The rapid leafing out resulted in a "closing in" of the forest canopy. During this period the ferns which made up much of the understory grew rapidly and nearly attained full size (approx. 1 m). The net effect was a marked reduction in the amount of light reaching the forest floor. Synchronization of circadian activity rhythms has been shown to be strongly affected by the day-

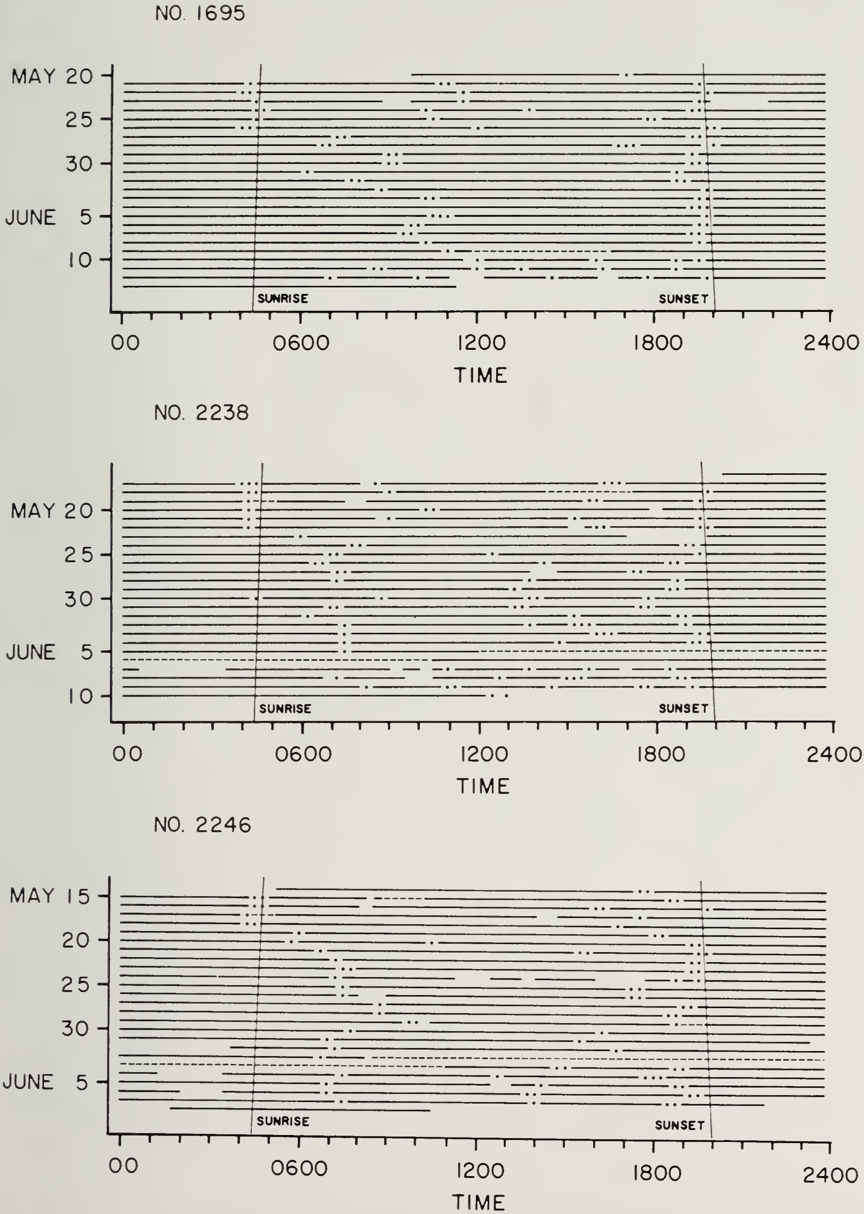

FIG. 4. Daily periods of activity during the incubation period for Hens 1695, 2238, and 2246 (—— = inactive, · · · = active, – – – = known disturbances by humans, blank = no data).

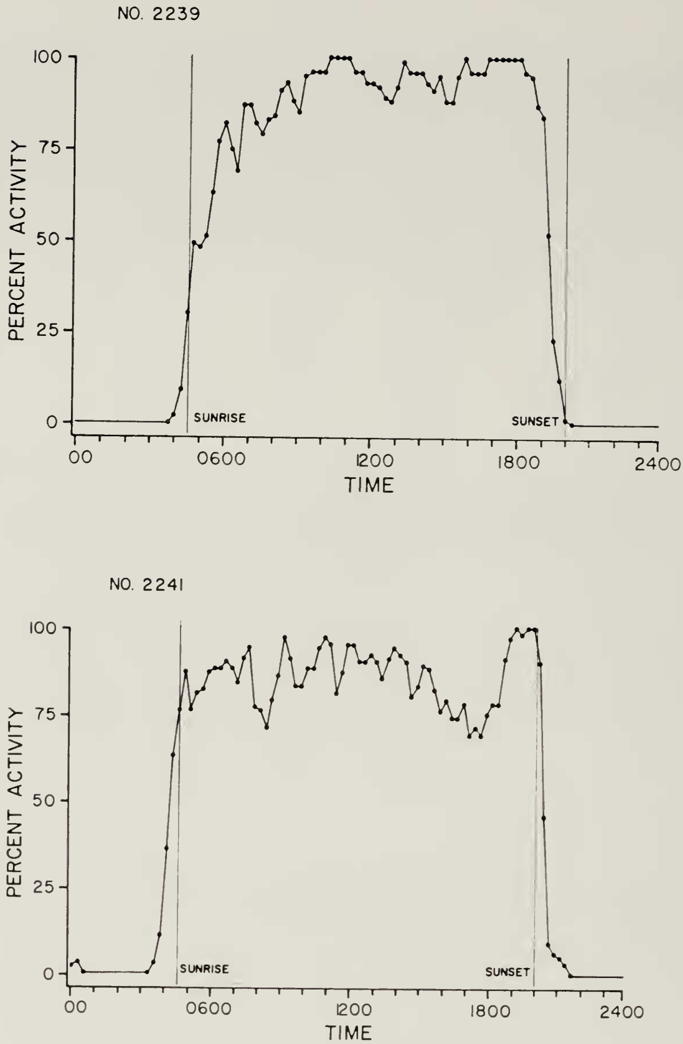

FIG. 5. Temporal distribution of percentage of 15-min intervals active during the post-incubation period for Hen 2239 (with brood) and Hen 2241 (no brood).

night cycle of illumination (Aschoff 1966). If the onset of morning activity during incubation is associated with light intensity at the nest, activity would likely start increasingly later as the tree canopy leafed over and herbaceous vegetation grew up around the nest.

On several occasions precipitation noticeably affected normal activity patterns. On 19 May 1971 a snow-rain storm from about 04:15–10:30 left a temporary accumulation of snow on the ground. Of 3 hens incubating at that time 2 did not leave the nest to feed until 14:00–14:15. The third remained on the nest until 17:30. Rain occurred during most of the morning hours on 29 May 1972. Several hens including 2238 and 2246 (Fig. 4) delayed or omitted the normal morning feeding period. On another occasion, at the onset of a hard rain shower, several hens which had been feeding returned to their nests almost immediately. This behavior is adaptive since egg temperatures are maintained during periods when rapid chilling would probably occur if the hen was absent.

Post-incubation.—Temporal distribution of percentage of 15 min intervals active during the post-incubation period was determined for 7 hens with broods and 4 broodless hens which had lost clutches to predators (Maxson 1974). As examples of these data Fig. 5 illustrates the activity patterns of Hen 2239 (with brood) and Hen 2241 (no brood). With but a single exception (Hen 2202), once activity peaked in the morning the birds maintained a high percentage of activity throughout most of the daylight hours until activity ceased in the evening. These daytime levels of activity were often higher than those observed during the pre-incubation period. Evening activity peaks tended to be greater than early morning peaks, but the pattern was not so consistent as during pre-incubation.

A difference in timing of the dawn-dusk peaks between hens with broods and those without broods was readily apparent. Brood hens did not attain the morning activity peak until 1–2¾ h after sunrise. The evening peak occurred 15 min–2 h prior to sunset. Broodless hens reached morning activity peaks 15–30 min after sunrise and evening peaks from 15 min before to 15 min after sunset.

Daily activity during the post-incubation period is illustrated for Hens 2239 and 2241 in Fig. 6. Hen 2239 began activity 2–3 h after sunrise during the first few days following hatching of the chicks. Thereafter, the onset of activity became progressively earlier until it approached sunrise on the 13th day. An almost identical pattern was exhibited by all brood hens. For the post-incubation period as a whole, brood hens began activity after sunrise on 101 of 114 (88.6%) grouse-days. Activity ceased prior to sunset on 104 of 115 (90.4%) grouse-days. In contrast, broodless hens initiated daytime activity prior to sunrise on 74 of 105 (70.5%) grouse-days and ceased activity after sunset on 55 of 83 (66.3%) grouse-days.

No doubt the delaying of morning activity onset and early evening activity cessation by brood hens is related to brooding of the chicks during cooler

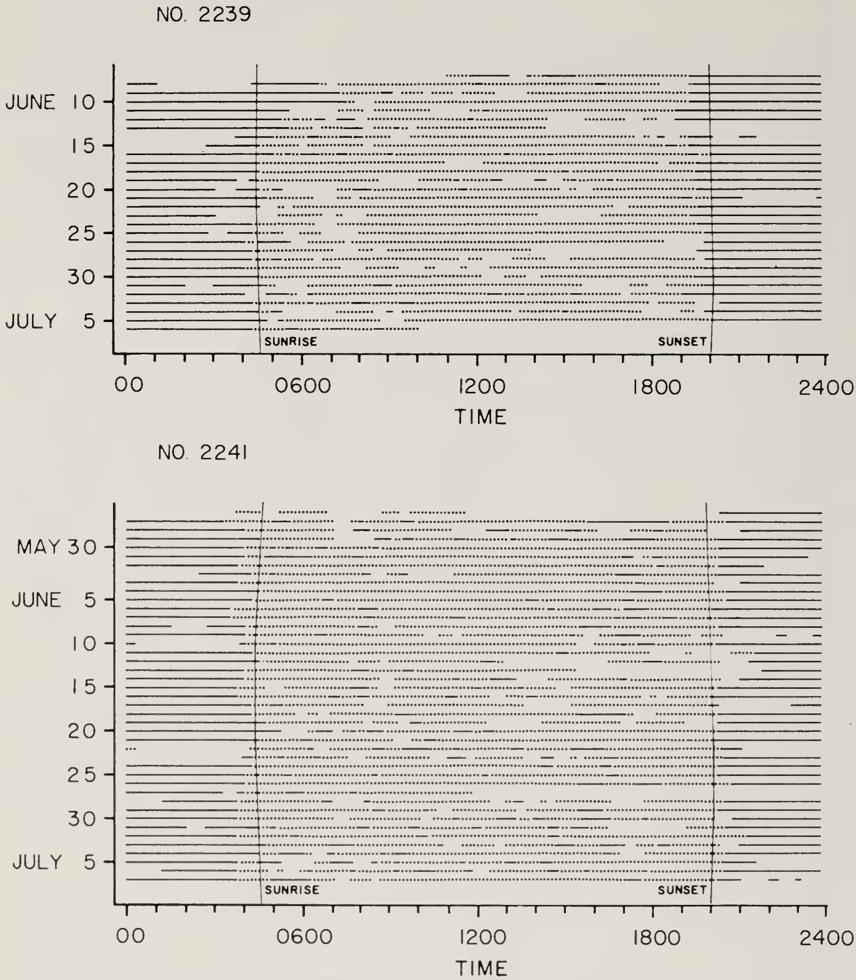

FIG. 6. Daily periods of activity during the post-incubation period for Hen 2239 (with brood) and Hen 2241 (no brood) (—— = inactive, · · · = active, blank = no data).

periods of the day. Brooding at these times was most pronounced during the first few days when chicks were least able to maintain body temperatures. Young chicks moving about during early morning hours would be exposed to wetting and rapid chilling due to heavy dew normally present. As the chicks grew older and more independent of the brooding hen, activity patterns of these hens gradually began to resemble those of broodless hens.

DISCUSSION

A major concern of telemetry studies is that the transmitter may cause behavioral changes in the study animals. Since many telemetry studies are conducted on animals difficult to observe in the wild, effects of the transmitter on behavior are difficult to determine. Boag (1972) stated that activity levels as well as food intake by captive female Red Grouse (*Lagopus l. scoticus*) were lower among radio-marked birds than controls, especially during the first week after transmitter attachment. At Cedar Creek properly fitted transmitter harnesses had no noticeable effects on behavior of Ruffed Grouse. The harnesses fitted so well that within a short time after release only the whip antenna on the bird's back was visible. During field observations it was not possible to distinguish marked from unmarked birds unless the whip antenna could be seen. Observations of captive grouse at Cedar Creek by Huempfner and Maxson (unpubl. data) also failed to reveal behavioral differences between marked and unmarked birds.

Data concerning Ruffed Grouse activity are available from several telemetry studies. Huempfner (unpubl. data) found that mid-day activity during the winter months (especially when birds were able to snow-burrow roost) was substantially lower than mid-day activity levels recorded during the present study. Brander (1965) reported that radio-marked Ruffed Grouse, in the absence of sufficient snow for burrowing, roosted at sunset and left the roost about 30 min before sunrise during March and April. His birds were inactive from mid-morning until mid-afternoon especially during March. The inactive periods probably reflect the need to conserve energy during the winter months. Schladweiler (1965) stated that Ruffed Grouse generally began activity 30–60 min before sunrise and ceased activity 30–60 min after sunset during the breeding season. Once activity began his birds tended to remain active most of the day without any prolonged inactive periods. Weather disturbed them little except when chicks were small. Probably a transition from prolonged mid-day inactive periods (Brander 1965, Huempfner unpubl. data) to few inactive periods during daylight hours (Schladweiler 1965, the present study) occurs during spring as temperatures increase and snow cover disappears.

The pattern of activity found in the present study (Figs. 1 and 5) is similar to the 2-peak activity pattern reported for several species of day-active birds by Aschoff (1966). The pattern of dawn peaks usually being lower than the dusk peaks was also evident in the data of other Cedar Creek researchers, e.g. Archibald (1973) for male grouse during spring and Pierson and Tester (unpubl. data) for several grouse of both sexes during November. This may prove to be the normal pattern throughout the year in this species. These morning and evening activity peaks are probably associated with feeding periods. Archibald (1973) observed male grouse feeding in trembling aspen (*Populus tremuloides*) clones during these times. On several occasions in the present study, I observed female grouse feeding in male aspen clones during the morning and evening activity peaks.

Egg laying.—Egg laying patterns similar to those of the present study (Figs. 2 and 3) have been found in domestic chickens (*Gallus gallus*) (Warren and Scott 1935, Scott and Warren, 1936), and pheasants (*Phasianus colchicus*) (Labisky and Jackson 1966). Warren and Scott (1935) stated that differences in time intervals between eggs in a sequence were probably due to differences in the time an egg spends in the uterus. Scott and Warren (1936) determined that skipping of one or more days between laying sequences was caused by a delay in ovulation of the first egg of a sequence rather than by overnight retention of a fully developed egg in the uterus. Probably the Ruffed Grouse follows a similar pattern of delaying ovulation between laying sequences.

The tendency for hens to remain inactive on the nest during laying visits for longer periods as the clutch neared completion was also noted in Spruce Grouse (*Canachites canadensis franklinii*) (McCourt et al. 1973).

Incubation.—Bump et al. (1947:288–289), Kupa (1966), and Schladweiler (1968) reported that incubating Ruffed Grouse usually left the nest for short periods, only a few times per day, as I found in the present study (Table 2, Fig. 4).

Skutch (1962) stated that, with the exception of certain nidifugous species, most birds which incubate alone cover their eggs 60–80% of the daytime. Tetraonids of at least several species exhibit nest attentiveness greater than 80%. In the present study, hens averaged 95.7% of the incubation period on the eggs. Kupa (1966) stated that Ruffed Grouse hens spent an average of 23 h and 12 min (96.7%) on the nests each day. Lennerstedt (1966) reported that a Capercaillie (*Tetrao urogallus*) hen, during 12 days of its incubation period, was off the nest only 4.9% of the time. McCourt et al. (1973) stated that 2 incubating Spruce Grouse spent 93% of daylight hours on the nest.

The shift in timing of the first activity period of the day exhibited by all hens in the present study (Fig. 4) has not been noted by other researchers. Lennerstedt (1966) reported that activity periods of an incubating Capercaillie were fairly evenly distributed throughout the day except from 18:00–23:00 when no absences occurred. Although his study was conducted under conditions of continuous daylight the data indicate that onset of activity periods between 03:00–06:00 gradually shifted from slightly after 03:00 to about 05:20 over the period of study. This shift is similar to that observed during my study but more data are needed to determine if the pattern is consistent among birds.

SUMMARY

Seventeen female Ruffed Grouse were equipped with radio transmitters and monitored with an automatic radio tracking system. Activity data were divided into pre-incubation, incubation, and post-incubation periods for each hen.

During the pre-incubation period peaks of activity were closely associated with sunrise and sunset. The evening peak was greater than the morning peak for all hens. Activity normally began 30–60 min prior to sunrise and ceased 15–45 min after sunset. Daytime activity seldom fell below the 50% level.

Egg laying patterns were determined for 8 hens. Hens seldom visited the nest site prior to the onset of egg laying and, once laying began, were rarely near the nest except during presumed laying visits. During laying visits hens typically remained inactive on the nest from 1 to several hours. Laying visits occurred 1–5 days in succession at 25–30 h intervals. When the next egg of a sequence appeared to be due sometime after the end of evening activity the egg was not laid until the following morning.

Evidence is presented that one hen successfully renested.

During incubation hens most often left the nest 2 or 3 times per day to feed. Most birds averaged 18–24 min per absence and 57–70 min off the nest per day. All hens exhibited a change in timing of the first activity period of the day as incubation progressed. This activity change may be related to plant phenology.

During post-incubation, once activity began in the morning, birds usually maintained a high percentage of activity throughout most of the daylight hours until activity ceased in the evening. Evening activity peaks tended to be higher than morning peaks. Brood hens did not attain the morning peak until 1–2¾ h after sunrise. The evening peak occurred 15 min–2 h prior to sunset. In contrast, broodless hens reached morning peaks 15–30 min after sunrise and evening peaks from 15 min before to 15 min after sunset. This difference between hens with and without broods is related to brooding of the chicks during the cooler portions of the day by the brood hens.

ACKNOWLEDGMENTS

I wish to express sincere appreciation to David F. Parmelee, John R. Tester, and William H. Marshall for their invaluable advice and assistance throughout the course of this study. For the design, construction, and maintenance of the telemetry equipment I am indebted to Ralph Schuster, Richard Reichle, and Valerian Kuechle. I am grateful to Richard Huempfner, Gary Erickson, and D. Andrew Saunders for assistance with the field work. The cooperation of the many personnel of the Cedar Creek Natural History Area is gratefully acknowledged. This investigation was supported by the U.S. Atomic Energy Commission (C00-1332-108). I thank Lewis W. Oring and George-Ann Maxson for critically reviewing the manuscript.

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